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WEBER'S THEORY OF THE KERNLEITER

ALVIN M. WEINBERG

THE UNIVERSITY OF CHICAGO

The potential distribution about a kernleiter is determined according to Weber's method. It is shown that the distribution reduces to the solution of a telegrapher's equation when the volume of the external medium is small. The velocity of propagation as a function of the external volume is determined approximately. This involves the solution of the equation

$$\frac{[Y_0(k\xi)]'}{[J_0(k\xi)]'} = \frac{[\xi^{-a} Y_0(\xi)]'}{[\xi^{-a} J_0(\xi)]'}$$

where Y_0 and J_0 are Bessel functions, and roots of this equation are tabulated. The velocities thus found reduce to Lillie's values determined experimentally on the iron wire when the conducting medium is small. Deviations from these values are predicted for larger volumes.

Most of the mathematical discussions of the kernleiter* have begun with the assumption that the kernleiter could be replaced by an electrical network in which the transverse and longitudinal impedances had certain known values per centimeter. (See, however, Cremer, 1899; Bishop, 1937; Wilson, Macleod, and Barker, 1933). Such a network could be described by a telegrapher's equation, the solution of which gives the current and voltage distribution along the line.

This classical solution of the cable problem is one-dimensional, since it tells nothing about the radial distribution of currents at distances out from the kernleiter. Such information becomes important, however, in discussing the theory of one of R. S. Lillie's passive iron wire experiments (1925, 1936). Lillie enclosed a passive iron wire in a glass cylinder of radius a ; he then determined the velocity of propagation as a function of a . Since the action currents spread radially throughout the space between the wire and its enclosing jacket, one would suppose that the velocity of propagation should depend on the nature of this radial distribution. Lillie, in analyzing his experimental results, assumed that the current density was uniform throughout the space between the wire and the jacket. This is correct if, as in his

* By a "kernleiter" (core-conductor) we mean a cylindrical conductor covered by a sheath or membrane and immersed in an electrolytic medium. Nerve axon, the passive iron wire, and submarine cable fall into this category.

experiments, the jacket is not much larger than the wire; but if the radius a is much greater than the wire radius, the current density will not be uniform, but will fall off radially from the wire.

In this paper we shall determine the radial distribution of the currents, and we shall then calculate the velocity of an impulse insofar as it depends on this distribution. In our discussion, we shall follow the treatment of H. Weber (1873a) rather closely. Weber's work has long been recognized as a standard contribution by mathematicians and physicists (Watson, p. 787), but it seems to have been somewhat neglected by physiologists, perhaps because, at the time it appeared, the refined experimental techniques required to check his theoretical predictions were not available.

Stationary Distribution: Finite External Medium

We shall first find the stationary current and voltage distribution about a semi-infinite kernleiter of radius b covered with a sheath or membrane of effective conductivity $1/\tau$ in $\text{ohm}^{-1} \text{cm}^{-2}$, and surrounded by a glass cylinder of radius a , the intervening medium being filled with an electrolyte of specific resistance κ (Figure 1). For the passive

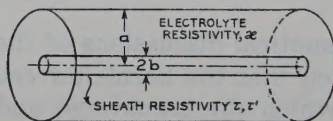


FIGURE 1

iron wire, the electrolyte, 70% HNO_3 , has a conductivity of about $1 \text{ ohm}^{-1} \text{cm}^{-1}$; this is only one millionth the conductivity of iron, and so the core of the wire will be assumed to be a perfect conductor at zero potential. Also, we shall assume that the current distribution is radially symmetric; the more general case in which the distribution depends on the azimuthal angle is treated in detail by Weber.

If u is the potential at some point in the medium, then u must satisfy Laplace's equation in cylindrical coordinates:

$$\frac{\partial}{\partial r} \left(r \frac{\partial u}{\partial r} \right) + \frac{\partial^2 u}{\partial z^2} = 0 \quad (1)$$

with the following boundary conditions:

At $r = a$, no radial current flow:

$$\frac{\partial u}{\partial r} = 0. \quad (2)$$

At $z = \infty$, potential is zero:

$$u = 0. \quad (3)$$

At $r = b$, current through the membrane sheath is equal to the current reaching the membrane from the electrolyte:

$$h \frac{\partial u}{\partial r} = u \quad (4)$$

where $h = \tau/\kappa$. This boundary condition corresponds to Kirchhoff's current law as used in the derivation of the telegrapher's equation.

To complete the specification of the problem, the initial distribution of the current or voltage must be given. As an approximation to the physical situation that obtains when an annular element on the kernleiter surface is excited, we may suppose that at $z = 0$, the longitudinal current through the sheath is just the action current, while all other currents in the system are zero: i.e., at $z = 0$,

$$\frac{\partial u}{\partial z} = -\Phi(r) \quad (5)$$

where

$$\Phi(r) = \lim_{\Delta b \rightarrow 0} (\tau' I / 2 \pi b \Delta b) \quad \text{for } b < r < b + \Delta b;$$

$$\Phi(r) = 0 \quad \text{for } r > b + \Delta b;$$

I being the action current, Δb the thickness of the sheath through which the current flows, and τ' the specific resistance of the sheath in ohm cm. This, of course, is only an approximation to the actual initial condition; it will be seen presently that the exact form of this assumption is not very important for certain of our purposes. (The function u defined by (1)-(5) is essentially the Green's function (Smythe, p. 56) for the enclosed kernleiter.)

The solution of this problem is, according to Weber,

$$u(r, z) = \sum_i A_i f(x_i, r) e^{-x_i z} \quad (6)$$

where (after correcting Weber's normalizing factor)

$$f(x_i, r) = J_0(x_i r) Y_1(x_i a) - J_1(x_i a) Y_0(x_i r),$$

$$A_i = \int_b^a \Phi(r) f(x_i, r) r dr \quad / \quad x_i \int_b^a f^2(x_i, r) r dr \quad (7)$$

$$= \pi h^2 x_i \tau' I f(x_i, b) / [4h^2 - \pi^2 b^2 (1 + h^2 x_i^2) f^2(x_i, b)],$$

and the x_i are roots of the characteristic equation

$$\frac{Y_1(ax)}{J_1(ax)} = \frac{hx Y_1(bx) + Y_0(bx)}{hx J_1(bx) + J_0(bx)}, \quad (8)$$

the functions $J_i(bx)$ and $Y_i(bx)$ being Bessel functions of the first and second kinds, respectively (Watson, pp. 38, 63). The series (6) diverges at $z = 0$, but converges for $z > 0$; such behavior is characteristic of Green's functions.

The potential at $r = b$, which is just the voltage across the membrane, is found from (6) and (7):

$$u(b, z) = \pi h^2 \tau' I \sum_i x_i f^2(x_i, b) e^{-x_i z} / 4h^2 - \pi^2 b^2 (1 + h^2 x_i^2) f^2(x_i, b). \quad (9)$$

If the x_i increase sufficiently rapidly with i , or if z is large, only the first term of the expansion (6) need be kept:

$$u_1(r, z) = \frac{\pi h^2 \tau' I x_1 f(x_1, b)}{4h^2 - \pi^2 b^2 (1 + h^2 x_1^2) f^2(x_1, b)} f(x_1, r) e^{-x_1 z} \quad (10)$$

or

$$u_1(b, z) = u_0 e^{-x_1 z}, \quad (11)$$

where physically u_0 must be approximately the potential on the surface of the kernleiter at $z = 0$, the approximation improving as the ratio x_1/x_i , $i > 1$, decreases. Since u_0 has physical significance independent of any artificial assumptions about $\Phi(r)$, it is clear that to this degree of approximation the original initial condition is immaterial. It is seen from (10) or (11) that the potential falls off exponentially with length constant or characteristic length $1/x_1$; this result corresponds to the exponential distribution found along a cable characterized by a telegrapher's equation.

The Characteristic Equation

The characteristic equation (8) was not discussed at any length by Weber, and so we shall indicate in some detail how its roots may be approximated. If h is very small, (8) becomes

$$\frac{Y_1(ax)}{J_1(ax)} = \frac{Y_0(bx)}{J_0(bx)}, \quad (12)$$

while if h is very large, the equation reduces to

$$\frac{Y_1(ax)}{J_1(ax)} = \frac{Y_1(bx)}{J_1(bx)}. \quad (13)$$

Series for the roots of both these equations have been given in the literature (Kalähne, 1907; Sasaki, 1914), and the first few roots of (13) have been tabulated by Kalähne for various values of $k (=a/b)$.

A similar series for roots of (8) can be obtained by writing (8) as

$$\frac{[Y_0(ax)]'}{[J_0(ax)]'} = \frac{[x^{-b/h} Y_0(bx)]'}{[x^{-b/h} J_0(bx)]'} \quad (14)$$

(where primes denote derivatives with respect to x), and applying Stokes' method (McMahon, 1894); but the resulting series converges too slowly and is not convenient for calculation when k is large.

A rather neat method used by Kalähne to obtain roots of (13) can be modified to find as many roots of (8) as are needed for the expansion (9). Upon putting $\eta = ax$, $\xi = bx$, we can write (8)

$$Y_1(\eta) - R(\xi, b/h) J_1(\eta) = 0 \quad (15)$$

where

$$R(\xi, b/h) = \frac{h \xi Y_1(\xi) + b Y_0(\xi)}{h \xi J_1(\xi) + b J_0(\xi)}. \quad (16)$$

For any assigned value of ξ , $R(\xi, b/h)$ is a function of b/h alone, $R_\xi(b/h)$. Then for every value of b/h , $R_\xi(b/h)$ has some constant value, $R_{\xi, b/h}$, so that (15) becomes

$$Y_1(\eta) - R_{\xi, b/h} J_1(\eta) = 0. \quad (17)$$

Equation (17), for a preassigned value of ξ_i , is a fairly simple transcendental equation whose root of the j -th order, η_j , can be found with considerable accuracy from Watson's tables (where Y_1 and J_1 are listed in adjoining columns), and with greater accuracy from the British Association tables (1937). In this way a root of (8)

$$x_i = \xi_i / b \quad (18)$$

is found for a value of k given by

$$k = \eta_j / \xi_i. \quad (19)$$

Roots for intermediate values of k can be found by interpolation.

We shall now prove that for a fixed k and b/h , the order of x_i as a root of (8) is the same as the order of ξ_i as a root of

$$R_{b/h}(\xi_i) - R_{\xi, b/h} = 0. \quad (20)$$

To do this, we must first show that the values of ξ_i which satisfy (20) form a monotonic sequence in which the subscript i denotes the *period* (defined as a connected range of ξ over which $R_{b/h}(\xi)$ takes every arbitrary real value once and only once) in which ξ_i is found. These periods consecutively cover the entire positive real ξ -axis, since we can show that the poles and zeros of $R_{b/h}(\xi)$ are interlaced (Watson, p. 479); this is true since (cf. equations (24), below)

$$\frac{dR}{d\xi} = \frac{2}{\pi\xi} \left[\frac{h^2}{b^2} \xi + 1 \right] / \left[\frac{h\xi}{b} J_1(\xi) + J_0(\xi) \right]^2,$$

being always positive for $\xi > 0$, implies that $R_{b/h}(\xi)$ is monotonically increasing. Therefore, *the zeros and poles of R are interlaced, and the entire positive ξ - axis is covered by periods in each of which a solution of (20) occurs once and only once (Figure 2).* The justifica-

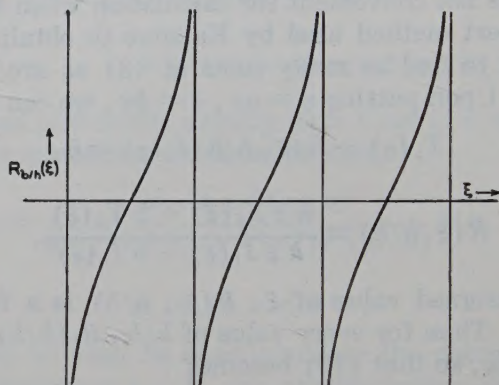


FIGURE 2

tion for referring to i as the "order" of ξ_i as a root of (20) lies in this result.

We can now show that the order of x_i as a root of (8) is the same as the order of ξ_i as a root of (20) if we can prove that for a fixed k , the function

$$\Psi(\xi) = Y_1(k\xi) - R_{b/h}(\xi) J_1(k\xi)$$

is monotonic in $\xi (= x/b)$. For if Ψ is monotonic, its poles will again divide the ξ - axis into periods over each of which Ψ monotonically takes on all real values. But the poles of Ψ are identical with the poles of $R(\xi)$, and so *the i -th zero of Ψ and the i -th zero of $R_{b/h}(\xi) - R_{\xi, b/h}$ must occur in the same period.*

To prove that $\Psi(\xi)$ is monotonic, we first suppose that $\Psi(\xi)$ has a horizontal tangent and then show that this leads to a contradiction. If Ψ has a horizontal tangent, then for at least one value of b/h , Ψ must have a multiple root. But since the functions $f(x_i, r)$ and $f(x_j, r)$ are orthogonal (Weber, 1873a) whenever $x_i \neq x_j$ but are identical if $x_i = x_j$, and since this is true regardless of the value of b/h , it follows that Ψ cannot have a multiple root for *any* value of b/h , and so Ψ must be monotonic.

In actually calculating the roots, we start with an arbitrary small value of ξ and ascertain its order as a root of (20) by inspecting Watson's tables. Corresponding values of η are found by trial, and from

these, values of k can be computed [equation (19)]. First order roots computed in this way for several values of k and $b = .1588$ cm. (1/16 inch), $h = 1$ cm., are shown in Table I. Higher order roots for $k = 20$ and the same values of b and h are given in Table II, and x_i versus k graphs which were used in constructing Table II are given in Figure 3.

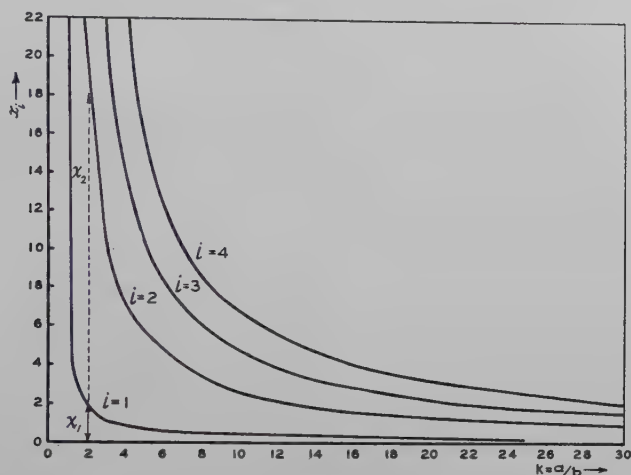


FIGURE 3

Characteristic values, x_i versus k . Note that $x_i - x_1$ increases as k decreases.

TABLE I: First order roots of (8) compared with x_Δ

$h = 1$ cm., $b = .1588$ cm.

$k = a/b$	x_1	$x_\Delta = [2b/h(a^2 - b^2)]^\dagger$
1.020	17.63	17.59
1.039	12.59	12.58
1.147	6.30	6.32
1.50	3.15	3.18
1.705	2.52	2.57
1.91	2.14	2.19
2.10	1.89	1.94
2.33	1.64	1.69
2.88	1.26	1.32
3.93	0.882	.936
5.30	0.630	.681
12.45	0.252	.286
23.90	0.126	.149

TABLE II: Higher order roots of (8) for $k = 20$,

$h = 1$ cm., $b = .1588$ cm.

k	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8
20	.14 ₉	1.2 ₄	2.2 ₇	3.2 ₉	4.3 ₁	5.3 ₃	6.3 ₄	7.3 ₃

If the difference $a - b$ is small (i.e. $k \infty 1$) the current density should be practically uniform throughout the external medium. The longitudinal resistance per centimeter in this case is $\kappa/\pi(a^2 - b^2)$ and so x_Δ , the reciprocal of the characteristic length *as calculated from the usual telegrapher's equation* (Weinberg, 1940) is

$$x_\Delta = \sqrt{\frac{M}{s}} = \sqrt{\frac{2b}{h(a^2 - b^2)}}, \quad (21)$$

where M is the longitudinal resistance per centimeter, and $1/s$ is the transverse conductance per centimeter. The first order root of (8) must reduce to x_Δ in this case; we can prove this as follows:

If $a = b + \Delta$, ($\frac{\Delta}{b} \ll 1$), then by Taylor's theorem

$$\begin{aligned} Y_1(ax) &= Y_1(bx + \Delta x) \approx Y_1(bx) + \Delta x Y_1'(bx) + \frac{\Delta^2 x^2}{2} Y_1''(bx) \\ J_1(ax) &= J_1(bx + \Delta x) \approx J_1(bx) + \Delta x J_1'(bx) + \frac{\Delta^2 x^2}{2} J_1''(bx). \end{aligned} \quad (22)$$

If these expressions are substituted into (8) we find, after clearing fractions and using certain identities between Bessel functions of the first and second kinds,

$$x \left(\frac{h \Delta^2}{b} - \Delta^2 - 2h \Delta \right) + \frac{1}{x} \left(2 - \frac{2\Delta}{b} + \frac{2\Delta^2}{b^2} \right) = 0. \quad (23)$$

The identities used in obtaining (23) are (Watson, p. 76)

$$\begin{aligned} J_n(\xi) Y_n'(\xi) - Y_n(\xi) J_n'(\xi) &= 2/\pi \xi \\ J_n(\xi) Y_n''(\xi) - Y_n(\xi) J_n''(\xi) &= -2/\pi \xi^2 \\ J_n(\xi) Y_n'''(\xi) - Y_n(\xi) J_n'''(\xi) &= \frac{2}{\pi \xi} \left(\frac{n^2 + 2}{\xi^2} - 1 \right). \end{aligned} \quad (24)$$

Equation (23) is a quadratic in x which has the positive root

$$x = \sqrt{\frac{2(b^2 - b\Delta + \Delta^2)}{\Delta b(2hb - h\Delta + b\Delta)}} \quad (25)$$

this being a second approximation to the first root of (8). If $(\Delta/b)^2$ be neglected in comparison with Δ/b , the root becomes

$$x = \sqrt{\frac{2b - a}{hb(a - b)}} \quad (26)$$

and since $\lim_{\Delta \rightarrow 0} \frac{a+b}{2} = b$,

$$\lim_{\Delta \rightarrow 0} x = x_{\Delta}.$$

In the limit, the length constant in the exact theory is identical with that of the simple telegrapher's theory [cf. Carslaw (1906), p. 322, and Table II above]. Moreover (Figure 3), the ratio x_1/x_i ($i > 1$) decreases with k so that when $k \infty 1$, only the first term of (9) remains, and the solution of the present partial differential equation reduces to the solution of the simple telegrapher's equation.

We should expect the fall of potential along the line to be more gradual for a uniform radial current distribution than for the actual current distribution, since the rate of fall of potential is measured by the effective longitudinal conductance [equation (21)], and the effective conductance is overestimated by assuming a uniform distribution. Table I seems to contradict this result, for x_{Δ} [which by equation (21) is inversely proportional to the longitudinal conductance] is larger than the corresponding x_1 . The discrepancy becomes worse as k increases; that is, as the non-uniformity of the radial distribution becomes more pronounced. This apparent paradox is explained by the fact that when k becomes large, the higher order terms of (6) cannot be neglected (Table II). The resulting distributions fall to $1/e$ -th their value more rapidly than the simple exponential distribution (Figure 4), at least when z is so large that the effect of the sin-

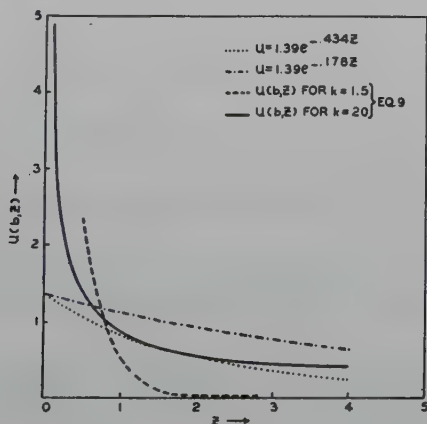


FIGURE 4

Distribution of $u(b,z)$ for $k = 1.5$ and $k = 20$, together with approximating exponentials for $k = 20$.

gularity at $z = 0$ becomes unimportant. We can therefore conclude from this analysis that *the effective longitudinal resistance of the external medium is larger than the resistance calculated on the assumption that the current density is uniform.*

Stationary Distribution: Infinite External Medium

If the kernleiter is immersed in an infinite medium, $a = \infty$, the calculation of the potential distribution requires the use of a certain generalized Fourier-Bessel integral. Weber discussed a problem of this sort in a later paper, (1873b), but he only treated the case $h = 0$. The generalization to the case at hand is rather immediate and involves nothing essentially new [cf. Carslaw and Jaeger, (1940)].

The problem to be solved is specified as before by equations (1)-(5), except that now $a = \infty$. (With $\Phi(r)$ chosen as an "impulse" function, the solution will again be a Green's function). Since the radial boundary is pushed out to infinity, we should expect the solution to involve something analogous to a Fourier integral (Watson, p. 576); in this respect the infinite problem is related to the finite problem just as the infinite vibrating string is related to the finite string.

A solution of (1) satisfying the boundary conditions (2), (3), and at (4) at $a = \infty$, $z = \infty$, and $r = b$ is

$$F(\alpha, r) e^{-\alpha z} = [h \alpha f_1(\alpha, r) + f_0(\alpha, r)] e^{-\alpha z} \quad (27)$$

where

$$f_i(\alpha, r) = (-1)^i [J_0(\alpha r) Y_i(\alpha b) - J_i(\alpha b) Y_0(\alpha r)]. \quad (28)$$

From this special solution we form the general solution by superposition:

$$u(r, z) = \int_0^\infty B(\alpha) F(\alpha, r) e^{-\alpha z} d\alpha \quad (29)$$

where, in order to satisfy (5), we must determine $B(\alpha)$ so that

$$\int_0^\infty \alpha B(\alpha) F(\alpha, r) d\alpha = \Phi(r). \quad (30)$$

The expansion (29) is analogous to a Fourier integral, but is somewhat more general. In order to determine $B(\alpha)$, we must find the inversion of (30).

Let us multiply both sides of (30) by $r F(\beta, r) dr$ and integrate between the limits b and ∞ . Then if $\Phi(r)$ is given by (5), we have

$$\int_b^\infty r \Phi(r) F(\beta, r) dr = \frac{h \tau' I}{\pi^2 b} \quad (31)$$

since $F(\beta, b) = 2h/\pi b$ (equation 24).

The left hand integral is, after interchanging the order of integration,

$$\int_b^\infty r F(\beta, r) dr \int_0^\infty \alpha B(\alpha) F(\alpha, r) d\alpha = \int_0^\infty \alpha X(\alpha, \beta) B(\alpha) d\alpha \quad (32)$$

where

$$X(\alpha, \beta) \equiv \int_b^\infty r F(\beta, r) F(\alpha, r) dr. \quad (33)$$

Since $F(\alpha, r)$ satisfies the original differential equation and boundary conditions, we find by integrating by parts,

$$X(\alpha, \beta) = \frac{1}{\alpha^2 - \beta^2} \lim_{r \rightarrow \infty} r \left\{ F(\alpha, r) \frac{dF(\beta, r)}{dr} - F(\beta, r) \frac{dF(\alpha, r)}{dr} \right\}. \quad (34)$$

If we substitute this expression into (32) we are led to consider the following limit:

$$\int_0^\infty \alpha X(\alpha, \beta) B(\alpha) d\alpha = \lim_{r \rightarrow \infty} \int_0^\infty \frac{\alpha B(\alpha)}{\alpha^2 - \beta^2} r \left\{ F(\alpha, r) \frac{dF(\beta, r)}{dr} - F(\beta, r) \frac{dF(\alpha, r)}{dr} \right\} d\alpha. \quad (35)$$

In this limit, the asymptotic values of $F(\alpha, r)$ and $dF(\alpha, r)/dr$ are required. These can be found by using the asymptotic expressions for the Bessel functions (Watson, p. 199)

$$\begin{aligned} J_n(\xi) &\sim \left(\frac{2}{\pi \xi} \right)^{\frac{1}{2}} \cos \left(\xi - \frac{1}{2} n \pi - \frac{1}{4} \pi \right) \\ Y_n(\xi) &\sim \left(\frac{2}{\pi \xi} \right)^{\frac{1}{2}} \sin \left(\xi - \frac{1}{2} n \pi - \frac{1}{4} \pi \right) \end{aligned} \quad (36)$$

in equation (35). After a lengthy set of manipulations, we obtain from (35) and (36)

$$\begin{aligned} \int_0^\infty \alpha X(\alpha, \beta) B(\alpha) d\alpha &= \lim_{r \rightarrow \infty} \frac{1}{\pi} \left\{ \int_0^\infty \frac{\alpha B(\alpha)}{\sqrt{\alpha \beta}} E(\alpha) \frac{\sin(\alpha - \beta)r}{\alpha - \beta} d\alpha \right. \\ &+ \int_0^\infty \frac{\alpha B(\alpha)}{\sqrt{\alpha \beta}} G(\alpha) \frac{\cos(\alpha + \beta)r}{\alpha + \beta} d\alpha + \int_0^\infty \frac{\alpha B(\alpha)}{\sqrt{\alpha \beta}} H(\alpha) \frac{\sin(\alpha + \beta)r}{\alpha + \beta} d\alpha \\ &\left. + \int_0^\infty \frac{\alpha B(\alpha)}{\sqrt{\alpha \beta}} K(\alpha) \frac{\cos(\alpha - \beta)r}{\alpha - \beta} d\alpha \right\} \quad (37) \end{aligned}$$

where

$$\begin{aligned} E(\alpha) &\equiv \Lambda(Y_1, Y_1, \beta, \alpha) + \Lambda(J_1, J_1, \beta, \alpha), \\ G(\alpha) &\equiv -\Lambda(J_1, J_1, \beta, \alpha) + \Lambda(Y_1, Y_1, \beta, \alpha), \\ H(\alpha) &\equiv -\Lambda(J_1, Y_1, \beta, \alpha) - \Lambda(Y_1, J_1, \beta, \alpha), \\ K(\alpha) &\equiv \Lambda(J_1, Y_1, \beta, \alpha) - \Lambda(Y_1, J_1, \beta, \alpha), \end{aligned} \quad (38)$$

and

$$\begin{aligned} \Lambda(R_1, S_1, \beta, \alpha) &\equiv h^2 \alpha \beta R_1(\beta b) S_1(\alpha b) - \\ &h[\alpha R_0(\beta b) S_1(\alpha b) + \beta S_0(\alpha b) R_1(\beta b)] + R_0(\beta b) S_0(\alpha b). \end{aligned} \quad (39)$$

The letters R_i and S_i stand for Bessel functions of either kind of order i .

The integrands of the last three integrals have no singularities on the range $0 \leq \alpha \leq \infty$. (The last integrand vanishes at $\beta = \alpha$ because $K(\beta) = 0$.) Consequently from Du Bois-Reymond's theorem of mean value (Whittaker and Watson, 1940; p. 66), the limit of each integral as $r \rightarrow \infty$ is zero. On the other hand, the first integral is an instance of Dirichlet's integral, and so (Whittaker and Watson, p. 176)

$$\begin{aligned} \int_0^\infty \alpha X(\alpha, \beta) B(\alpha) d\alpha &= \lim_{r \rightarrow \infty} \frac{1}{\pi} \int_0^\infty \frac{\alpha B(\alpha) E(\alpha) \sin(\alpha - \beta)r}{\sqrt{\alpha \beta} (\alpha - \beta)} d\alpha = \\ &B(\beta) E(\beta) \end{aligned} \quad (40)$$

or by the definition of $E(\alpha)$ [equations (38) and (39)],

$$\begin{aligned} \int_0^\infty \alpha X(\alpha, \beta) B(\alpha) d\alpha &= B(\beta) \{ [h\beta J_1(\beta b) - J_0(\beta b)]^2 \\ &+ [h\beta Y_1(\beta b) - Y_0(\beta b)]^2 \}, \end{aligned} \quad (41)$$

which is the value of the integral in (32). Setting this equal to the expression given in (31), we have

$$B(\beta) = \frac{h \tau' I}{\pi^2 b E(\beta)}, \quad (42)$$

and if we substitute this into (29), we obtain the required Green's function

$$\begin{aligned} u(r, z) &= \frac{h \tau' I}{\pi^2 b} \times \\ &\int_0^\infty \frac{F(\alpha, r) e^{-\alpha z}}{\{ [h\alpha J_1(\alpha b) - J_0(\alpha b)]^2 + [h\alpha Y_1(\alpha b) - Y_0(\alpha b)]^2 \}} d\alpha, \end{aligned} \quad (43)$$

which reduces to the function given by Weber in case $h = 0$. This integral converges whenever $z > 0$, but is divergent for $z = 0$; this behavior is analogous to that of the finite medium Green's function.

The value of u on the surface of the kernleiter sheath is found by putting $r = b$ in equation (43). Since $F(\alpha, b) = 2h/\pi b$, we have

$$u(b, z) = \frac{2h^2 \tau' I}{\pi^3 b^2} \times \int_0^\infty \frac{e^{-\alpha z}}{\{[h \alpha J_1(\alpha b) - J_0(\alpha b)]^2 + [h \alpha Y_1(\alpha b) - Y_0(\alpha b)]^2\}} d\alpha. \quad (44)$$

The integrals (43) and (44) cannot be evaluated exactly; however, if h is very large, an asymptotic expansion of (44) can be found. Since (Whittaker and Watson, p. 159)

$$\int_0^\infty \phi(\alpha) e^{-\alpha z} d\alpha \sim \frac{\phi(0)}{z} + \frac{\phi'(0)}{z^2} + \frac{\phi''(0)}{z^3} + \dots, \quad (45)$$

the first term in the asymptotic expansion of $u(b, z)$, in case h is large, is

$$u(b, z) \sim \frac{\tau' I}{2\pi z}, \quad (46)$$

while the next non-vanishing term is $\sim 1/z^5$ and so can be neglected. Unfortunately, this expansion cannot be used for small values of h , because (45) then becomes indeterminate.

From (46) we may conclude that *at distances sufficiently far from the electrodes, and for large values of h , the potential across the sheath falls off as $1/z$* . This result appears surprising in view of the usually accepted exponential distribution in cables. It may be argued that if the finite conductivity of the cable is taken into account, an exponential spread will result; but this is not the case, as Weber has shown (1873a). *If the conductivity of the core is finite, the current spread will still be given by a sum of exponentials which reduces to a single exponential only when the physical and geometrical parameters of the system insure that the current density is uniform.*

Propagation of the Impulse

In the present investigation we are interested primarily in two results: first, in the distribution of potential along the kernleiter, and second, in the effect of the size of the enclosing glass jacket on v , the velocity propagation. All of the formal conduction theories (Wein-

berg, 1940) start with an exponential current distribution in the derivation of the velocity formula; and while the resulting formulae differ in their dependence on certain excitation parameters, they all depend on the length constant, $1/x$, in the same way:

$$v \propto 1/x. \quad (47)$$

When k is not too large, Lillie's results seem to agree with this prediction (Figure 5); but if as in our case, the current distribution is only *approximately* exponential, formula (47) becomes somewhat meaningless.

Since we are not interested in the dependence of velocity on excitation parameters, and since, in simple cases, all the theories predict the same dependence on external resistance, we may choose the simplest excitation equation (Blair, 1932) in calculating the velocity:

$$\partial p / \partial t = u - \omega p \quad (48)$$

or its steady state equivalent

$$-v dp / d\zeta = u - \omega p,$$

where p is the excitation parameter which must exceed the threshold H , u is the membrane potential, $\zeta = z - vt$, and the voltage rheobase is ωE . For u we may substitute $u(b, z)$ from (9); if we then integrate (48) in the steady state, and set $p = H$ at $z = 0$, we find

$$\omega E = \sum \frac{\omega A_i}{\omega + vx_i} \quad (49)$$

where the A_i are defined in (7). Equation (49) is transcendental in v and so cannot be solved exactly, especially because of convergence difficulties at $z = 0$. If only the first term of (49) is used [cf. equation (11)], the usual expression for v is obtained (Weinberg, 1940)

$$v = \frac{u_0 - \omega E}{x_i E}. \quad (50)$$

Roughly, we would expect the velocity defined by (49) to be proportional to a "characteristic length" found by approximating the exact distribution (9) by an exponential over a portion of the z - range. Such approximating exponentials for $k = 20$ are included in Figure 4. Some ambiguity concerning the region of the u - curve to be approximated arises because of the singularity at $z = 0$; this difficulty can be partly overcome by requiring that the approximating curve lie above the u -curves found for $k < 20$ and below the u - curve which is the solution of the telegrapher's equation for $k = 20$.

Experimental Implications

An experimental study of some of the results contained in this paper seems to be within the range of present day techniques. For most of these experiments, the passive iron wire would be well suited; since the conductivity of its core is practically infinite compared to the surrounding nitric acid, our results would be more directly applicable to this model than to some of the collodion membrane kernleitors in which the core itself is an electrolyte.

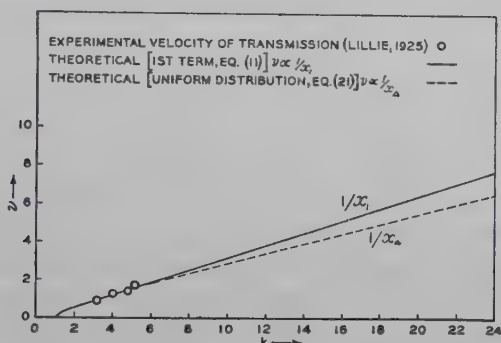


FIGURE 5

v versus k for passive iron wire: comparison of observed velocity in passive iron wire with values of $1/x_1$ and $1/x_A$. Note that $1/x_1$ is too large.

To check the general form of the potential distribution [equations (6) and (9)], h , the ratio of external to membrane conductivity, must be measured. This can be accomplished by determining, with probing electrodes, the potential distribution along the wire when the enclosing jacket just fits over the wire, and a polarizing current is applied through ring electrodes. Under these conditions a strictly exponential polarization spread should be found with length constant given by equation (21). If the polarization is plotted logarithmically against distance, a straight line whose slope is the characteristic length will be obtained, and from this slope the value of h can be found, if the acid conductivity is known (cf. Bogue and Rosenberg, 1934). The quantity h is related to the membrane structure, and so it should vary with the passivation time.

For a given passivation time, h should not depend on the size of the enclosing jacket. Consequently the value of h found for a small jacket can be used to calculate several roots of the characteristic equation (8) for large value of a ; the theoretical distribution can easily be found from (6), and this could be checked against the experimental polarization.

A further check on the validity of the relation between velocity and external resistance [equation (47)] can be obtained from the shape of the rising phase of the propagated action spike. It has been shown (Cole and Curtis, 1938; Offner, Weinberg, and Young, 1940) that the rising phase of the spike should be exponential with characteristic length, $1/x_v$, given by

$$x_v = \frac{1}{2}MCv + \sqrt{(MCv/2)^2 + M/s}, \quad (51)$$

where C is the transverse capacitance per centimeter of the membrane. When (K) is small, (50) becomes [cf. equation 21]

$$v = \sigma/\sqrt{M}, \quad (52)$$

σ being independent of jacket size. Equations (51) and (52) give

$$x_v/\sqrt{M} = \text{constant}; \quad (53)$$

if in experiments on the variation of velocity with k , the action spikes are recorded, relation (53) between the moving characteristic length and the external resistance should be found, at least when k is small. When k is large, a deviation from (53) is predicted; such a deviation, if discovered, would tend to confirm qualitatively the theory.

Finally, since the approximate "characteristic length" for large values of k is smaller than the corresponding x_Δ (Figure 4), the velocity of propagation should fall below the curve found by Lillie (Figure 5) when the glass jacket is large. Lillie's results were not extended beyond $k = 5$; up to this point the exact theory and the approximate theory predict almost identical results. Data on v versus k for larger values of k are needed to determine the validity of the present considerations.

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THE DYNAMICS OF CELL CONSTRICTION DURING DIVISION

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The approximate equation is derived for the rate of constriction of a dividing cell, describing the phenomenon from its early stages. The equation previously derived by G. Young for the case when the constriction has already considerably progressed is obtained as a limiting case.

The mechanism of cell constriction during division has been studied mathematically by G. Young (1939; c.f. also Rashevsky, 1940). An equation for the rate of constriction has been derived for the case when the constriction has already proceeded rather far. This equation has proved to agree rather well with available experimental data (Rashevsky, 1940, chap. iii). For the early stages of constriction no mathematical treatment has yet been available. By using the exact solution of the diffusion problem for an ellipsoid of revolution, and applying Betti's equation to different regions of the ellipsoid, G. Young (1939) was able to show that a constriction will set in, but no expressions for its variation with respect to time was derived for those early stages.

It is the purpose of the present paper to derive a crudely approximate, but general expression, which would describe the process of constriction in all its entirety. We shall follow the method used by G. Young for the case of already advanced constriction. One additional factor will be introduced, by way of correction to Young's argument.

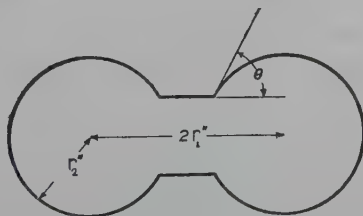


FIGURE 1

Consider the situation represented in Figure 1, in which the notations are obvious. This corresponds to G. Young's case (Young,

1939; Rashevsky, 1940, chap. iii). We shall now drop the restriction, used previously, namely that the radius r of the neck is small, compared to r_1 and r_2 . Before the constriction sets in, r may be as large as the smaller radius r_2 of the cell.

We have as before the force

$$F = \frac{R T \pi \mu q r_2''^6}{6 M D_e r_1''^2}, \quad (1)$$

which pulls on the neck. Even when the neck is very narrow, equation (1) is only a very rough approximation, obtained by neglecting the disturbance of the diffusion field of one sphere by the other. The same degree of approximation equation (1) may be used for the case, in which constriction has not yet set in. We may consider that the repelling force of each half of the cell is roughly the same as that of two closely adjacent spheres, with radii r_2 , where $2r_2$ is the average over all width of the cell.

To the force F is to be added the force

$$- 2 \pi r \gamma, \quad (2)$$

due to the lateral surface tension of the neck. In addition however a force is acting on the "ends" of the neck, namely the force

$$F' = - \frac{2 \gamma}{r_2''} \times \pi r^2 \quad (3)$$

due to the capillary pressure in the "spherical" parts. This term has not been taken into account by G. Young.

Furthermore there is a pull upon the "ends" of the neck equal to

$$2 \pi r \gamma \cos \theta = 2 \pi r \gamma \times \frac{r}{r_2''}, \quad (4)$$

due to the tangential component of the surface tension of the "spheres" at the edge of the neck, where the latter is connected to the "spheres". This force may be best combined with the force (2), giving as the total force due to tangential surface tension and directed along the axis of the neck

$$- 2 \pi r \gamma \left(1 - \frac{r}{r_2''}\right). \quad (5)$$

When the neck is narrow, $r < r_2$, we have only the term used by G. Young. When on the contrary, the constriction has not yet begun, this term is zero.

Altogether the forces (1), (3) and (5) are equivalent to an out-

ward directed pressure p_1 , applied to the "ends" of the neck, and equal to

$$p_1 = \frac{Fr_2'' - 2\pi\gamma r^2 - 2\pi\gamma r(r_2'' - r)}{\pi r_2''^2} = \frac{F - 2\pi\gamma r}{\pi r^2}. \quad (6)$$

At the "sides" of the neck we have the capillary pressure

$$p_2 = -\frac{\gamma}{r}, \quad (7)$$

as before. Applying now Betti's formula to the neck, and neglecting again the volume forces, which will be small due to the small length l of the neck, we find, just as before (G. Young, 1939; Rashevsky, 1940)

$$\frac{dr}{dt} = \frac{\gamma}{6\eta} - \frac{F}{6\pi\eta} \frac{1}{r}. \quad (8)$$

This is identical with Young's equation. However, by the nature of its derivation, it should hold even for the early stages of constriction. In fact, the comparison with experimental data (Rashevsky, 1940, chap. iii), which gave a rather good agreement, was carried out over a much wider range of values of r , than would have been permitted by the restriction to very advanced constriction.

The essential difference between our derivation and Young's is that we do first correct Young's argument for the capillary pressure term (3), which correction should hold for any degree of constriction; and second, introduce the term (4), which plays a role only when the constriction is small. The two terms compensate each other. If we do not introduce correction (3), but only correction (4), we would find

$$\frac{dr}{dt} = \frac{\gamma}{6\eta} - \frac{\gamma}{3\eta r_2''} r - \frac{F}{6\pi\eta} \frac{1}{r}, \quad (9)$$

which would reduce to Young's equation only for very small values of r .

One feels somewhat uncomfortable however in introducing a sharp angle between the "neck" and the "spheres". And if we consider that actually such an angle does not exist, but that the meridional line of the cell is a smooth curve, the whole argument which leads to expression (5) becomes rather doubtful, and even the original expression (2) used by Young loses its meaning. We shall therefore treat the problem in a different way, remembering that a positive pressure at the "ends" of the neck is equivalent to a corresponding negative pressure at the "sides".

We shall consider, as is actually the case, that the neck is negatively curved in the meridional plane, with an average radius of curvature r' . Then we have for the pressure p_1 at the "ends" of the neck:

$$p_1 = \frac{F}{\pi r^2} - \frac{2\gamma}{r_2''}, \quad (10)$$

and at the "sides":

$$p_2 = -\frac{\gamma}{r} + \frac{\gamma}{r'}. \quad (11)$$

Since, from Betti's formula

$$\frac{1}{r} \frac{dr}{dt} = -\frac{1}{6\eta} (p_1 - p_2), \quad (12)$$

therefore

$$\frac{dr}{dt} = \frac{1}{6\eta} \left(-\frac{F}{\pi r} - \gamma + \frac{2\gamma}{r_2''} r + \gamma \frac{r}{r'} \right). \quad (13)$$

The radius r' may be approximately calculated in the following way:

The quantities r_1'' and r_2'' are approximately connected with the overall length of $2r_1$ and the overall width $2r_2$ of the cell by

$$r_1 = r_1'' + r_2''; \quad r_2'' = r_2, \quad (14)$$

while the half length l of the neck is given by

$$l = r_1'' - r_2'' = r_1 - 2r_2. \quad (15)$$

Expression (15) holds only for $r_1 > 2r_2$. A more general but crude approximation may be made in the way indicated in Figure 3.

When the neck is very wide, the notion of length of the neck becomes somewhat indefinite. We shall use equation (15) as defining the length of $2l$ of the neck for any value of r .

For $r = r_2$ the radius r' is infinite. This at first seems to contradict the assumption made in the theory of cell elongation, according

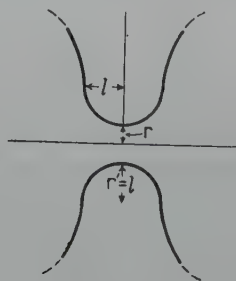


FIGURE 2

to which the mean curvature at the sides of the cell is taken to be $1/r_2 + 1/r_1$, which means $r' = -r_1$. We must remember however, that in the latter case we refer to the average mean curvature of the "sides". At present however we consider only the curvature in the meridional plane *near the equator*.

If during the process of constriction r_1 and r_2 remain approximately constant, then r' decreases from ∞ to a value approximately equal to l (Figure 2). This value is roughly reached when $r_2 - r$ becomes equal to l . Between $r_2 - r = 0$ and $r_2 - r = l$, the value of r' may be calculated from Figure 3, using the relation $r'/y = y/2x$, and is found to be equal to

$$r' = \frac{1}{2} \frac{(r_2 - r)^2 + l^2}{r_2 - r}. \quad (16)$$

From $r = r_2$ to $r = r_2 - l$ the value (16) should be used in equation (13). For $r < r_2 - l$, the value $r' = l$ is to be used. For very small values of r the first term of the right hand side of (15) prevails, and equation (15) reduces to that of Young. The condition for the con-

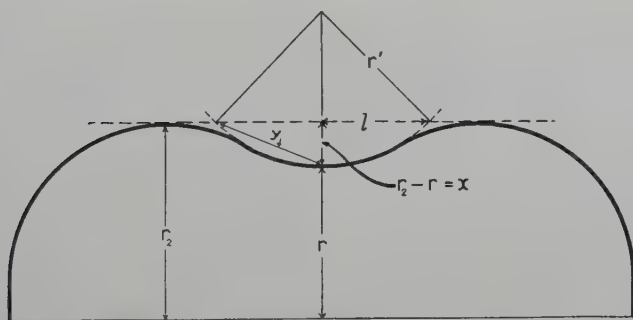


FIGURE 3

striction to occur at all is obtained by requiring $dr/dt < 0$ for $r = r_2$. This gives

$$F > \gamma \pi r_2, \quad (17)$$

or, because of (1) and (14)

$$\frac{R T \mu q r_2^5}{6 M D_e \gamma (r_1 - r_2)^2} > 1, \quad (18)$$

a relation that can be satisfied with plausible values of the constants.

If relation (18) is satisfied, then the constriction once started for $r = r_2$, will proceed until complete separation.

The author is indebted to Mr. H. D. Landahl for checking the calculations.

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A THEORY OF STEADY-STATE ACTIVITY IN
NERVE-FIBER NETWORKS:
I. DEFINITIONS AND PRELIMINARY LEMMAS

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As an essay towards the determination of the effect of structural relations among nerve fibers upon the character of their activity, preliminary consideration is given to the steady-state activity of some simple neural structures. It is assumed as a first approximation that while acted upon by a constant stimulus, each fiber reaches a steady-state activity whose intensity is a linear function of the applied stimulus. It is shown by way of example that for a simple two-fiber circuit of inhibitory neurons knowledge of the stimuli applied to the separate fibers does not necessarily suffice to determine uniquely the activity that will result. On the other hand, there are deduced certain restrictions on the possible types of activity that may be consistent with a given pattern of applied stimulation.

Studies in the mathematical biophysics of the nervous system by Rashevsky (1938, 1940; also various papers in *Psychometrika* and the *Bulletin of Mathematical Biophysics*), Landahl, and Householder (in the same periodicals) have presupposed certain equations as describing the dynamics of individual nerve fibers, and have deduced from these presuppositions the equations which would describe the behavior of certain nerve-fiber complexes of specified structure. These equations express the time course of the response of the efferent fibers of the complex in terms of the intensity of the stimulus applied to the afferent fibers, so that if the response of the organism depends in a known fashion upon the response of these efferent fibers, and if the intensity of the stimulus which acts upon the afferent fibers is given in terms of the external stimulus, then the response of the organism can be said to have been derived as a function of the external stimulus.

Hitherto all derivations have been made on the basis of special structural assumptions with no attempt at greater generality. Nevertheless, if we neglect conduction time (along the fiber), which is certainly legitimate to at least a first approximation, the behavior of any complex of nerve fibers must depend alone upon the dynamic properties of the individual fibers and the structural relations among these fibers. (The possibly variable physiological state of the organism as a whole, which may well effect the activity of some or all of the constituent fibers, is here assumed to constitute a part of the acting stimu-

lus.) Hence there must necessarily exist certain general propositions which express the activity of any nerve-fiber complex in terms of the dynamics of the individual fibers and of the structural constants. The present paper serves as an initial step towards the search for such propositions.

Naturally steady-state activity under constant stimulation is the simplest to consider; with this we therefore begin and to this we confine the present paper. That is, if a constant stimulus is applied for a period of time to each of certain fibers of the complex, whatever the fibers may do in the first few milliseconds, or even seconds, we suppose they settle down shortly to a steady response which persists unchanged as long as the stimuli are left unchanged. It is this steady-state behavior that we investigate here.

We *assume*, as a first approximation, that the steady-state activity of each fiber is a linear function of the intensity of the stimulus applied to it. Since this necessarily vanishes when the stimulus falls below a certain intensity which we here call the threshold (and which might conceivably exceed the true threshold), it follows that the response is to be taken as proportional to the amount by which the stimulus exceeds the threshold.

If a nerve fiber is stimulated at several points, and if the steady-state response is additive, as we *assume*, it is no restriction to think of the single fiber as replaced by several, one passing from each dendritic to each axonic synapse of the fiber. We therefore suppose that each fiber of the complex has but a single initial or afferent or dendritic synapse, and but a single terminal or efferent or axonic synapse. We further suppose that given any two synapses, say s_1 and s_2 , not more than one fiber has s_1 as its initial and also s_2 as its terminal synapse, and moreover that no fiber initiates and terminates in the same synapse. This is no real restriction, for any single fiber can be replaced by two or more in a chain, and the assumption is made for notational convenience only.

For if there are n synapses, designated by s_1, s_2, \dots, s_n , and if there is a fiber leading from s_i to s_j , we may denote it by $[i j]$, since there can be no more than one. Then at any given synapse, s_j , suppose there is applied a stimulus of constant intensity, S_j , positive, negative (inhibitory), or zero, from a source external to the complex itself and therefore independent of its activity. If constant stimuli are being applied at the same time to other synapses of the complex, and if there are fibers $[i j]$ terminating in s_j , then some of these may have been set into activity. If so the effective stimulus acting upon any fiber $[j k]$ initiating at s_j will be, not S_j , but the sum of S_j and the amounts of $\varepsilon - j$ produced by these fibers. Let η_j represent the

value of this sum after the system reaches its steady state. In the final steady state for the system each fiber $[i j]$ will be acted upon by an effective stimulus of amount η_i and produces $\varepsilon - j$ in an amount equal to $\alpha_{ij}(\eta_i - h_{ij})$. Here h_{ij} is the threshold of the fiber $[i j]$, and therefore essentially positive, while

$$\alpha_{ij} = \begin{cases} 0 & \text{when } \eta_i \leq h_{ij}, \\ \alpha_{ij} & \text{when } \eta_i > h_{ij}. \end{cases} \quad (1)$$

The parameter α_{ij} is a characteristic of the fiber which may be called its activity parameter. It is assumed to be different from zero, but it may be either positive (when the fiber is excitatory in character) or negative (when the fiber is inhibitory in character). Thus, since at each synapse the value of η is equal to a sum of the S applied from without the system, and the amounts of $\varepsilon - j$ produced by the active afferent fibers, it follows that

$$\eta_j = S_j + \sum_i \alpha_{ij}(\eta_i - h_{ij}). \quad (2)$$

The summation is extended over all values of i for which there exists a fiber $[i j]$, and the coefficients α_{ij} are defined by (1). Since the α 's are themselves functions of the η 's, these equations do not constitute a simple linear system, but rather present, for any given set of values of the S_j , a set of linear systems, one for each choice of a set of α 's to be taken as non-null, and among this set at least one system will presumably be such that the solutions η will be consistent with the conditions (1). But there is no assurance in advance that only one such choice of the non-null α 's will yield η 's as defined by (2) which are consistent with (1). In fact, a simple example will be exhibited below in which there are certainly more than one—at least for suitable S — values. In other words, the S — values may not define uniquely the steady state activity of a given nerve-fiber network. Instead, it may be necessary to know in addition the order in which the stimuli S_i are applied, or the rapidity with which the various fibers of the complex are capable of reaching their own steady states.

For a given system of nerve fibers let the values S_i of the stimuli externally applied be called the stimulus pattern SP . Let the values of the η_i be called the excitation pattern EP . And let the values of the α_{ij} constitute the activity pattern AP . Hence the general problem is to determine, for any given SP , every possible AP (or EP) that is consistent with (1). We remark in passing that when the structure of the system and the values of the parameters α_{ij} and h_{ij} are known,

then for any *EP*, the *AP* can be determined by (1) and the necessary *SP* by (2), both uniquely.

We note now that for a simple chain of fibers [12], [23], ..., $[n-1, n]$ the *AP* and the *EP* are uniquely and easily determined by the *SP*. For the activity of [12] and hence the value of η_2 depends upon S_1 alone; the activity of [23] depends upon η_2 alone; and so on to η_n . We therefore no longer need to consider a simple chain. If the system contains a simple afferent chain leading, say, to s_i , we may disregard it and consider S_i as including the contribution of this chain. If the system contains a simple efferent chain leading, say, from s_j , we may disregard it since the activity or non-activity of the fibers of this chain can have no effect on the rest of the system. Hence, we are led to consider only such systems containing synapses s_j ($j = 1, \dots, n$) such that every synapse joins at least one afferent fiber $[i j]$ belonging to the system to at least one efferent fiber $[j k]$ belonging to the system. We suppose, moreover, that given any two synapses s_i and s_k there is at least one chain $[i j_1], [j_1 j_2], \dots, [j_v k]$ leading from s_i to s_k and also one leading from s_k to s_i . Hence, the system does not consist of two separated subsystems, nor does it consist of two subsystems, say *A* and *B*, of such a nature that while there are fibers or chains leading from synapses in *A* to synapses in *B*, there are none leading from synapses in *B* to synapses in *A*. Such a system, whose every synapse joins an afferent to an efferent fiber, and whose every pair of synapses is joined by chains going both ways, we shall call a *fiber network*, and these alone we consider hereafter. The discussion of any other system can be reduced to the discussion of one or a chain of such networks.

The simplest possible network is a simple circuit of n fibers [12], [23], ..., $[n, 1]$. Discussions have already been given of the non-steady-state activity of a single self-exciting fiber (Landahl and Householder, 1939), and of a pair of mutually exciting fibers (Householder, 1938), both excitatory. It is easy to see that

If all fibers of a simple circuit are excitatory, then not more than one AP (EP) can be consistent with any given SP.

For a simple circuit we may simplify the notation somewhat, dropping the second subscript on the symbols α , a and h , so that

$$\alpha_i \equiv \alpha_{i,i+1}, \quad a_i \equiv a_{i,i+1}, \quad h_i \equiv h_{i,i+1}. \quad (3)$$

(All subscripts may be reduced modulo n .) Then define the quantities

$$\begin{aligned} \sigma_i &\equiv \sigma_i^{(1)} \equiv S_i - h_i, \\ \sigma_i^{(v)} &\equiv \sigma_i^{(1)} + a_{i-1} \sigma_{i-1}^{(v-1)}. \end{aligned} \quad (4)$$

Evidently

$$\sigma_i^{(v)} = \sigma_i^{(a)} + \alpha_{i-1} \cdots \alpha_{i-a} \sigma_{i-a}^{(v-a)}. \quad (5)$$

Also let

$$y_i \equiv \eta_i - h_i. \quad (6)$$

Then for the simple circuit the equations (2) reduce to

$$y_i = \sigma_i + \alpha_{i-1} y_{i-1}. \quad (7)$$

If the fibers are all excitatory, the activity of any one cannot decrease the activity of the succeeding one. Hence if every $\sigma_i \leq 0$, no fiber will be active. If every $\alpha_i > 0$ then every fiber must be active, every $\alpha_i = \alpha_i$, and (7) can be solved by ordinary methods. In the remaining alternative there will be some positive and some negative σ 's. Suppose $\sigma_j \leq 0$. If $[j, j+1]$ becomes active it can be only after and because $[j-1, j]$ has become active. Now starting with each σ_{j+1} which follows a non-positive σ_j , form the sequence

$$\sigma_{j+1}^{(1)} = \sigma_{j+1}, \sigma_{j+2}^{(2)}, \dots, \sigma_{j+v}^{(v)}, \quad (8)$$

terminating with the first non-positive term (which may be σ_{j+1} itself), or else with $\sigma_j^{(n)}$. If, among these sequences, there is one which contains all n terms, then either the last term, $\sigma_j^{(n)}$, is non-positive, in which case the solutions y of (7) are given by the members of this sequence,

$$y_{j+a} = \sigma_{j+a}^{(a)}, \quad (9)$$

or else the last term $\sigma_j^{(n)}$ is positive and all fibers are active, the *EP* being given by (7) with $\alpha_i = \alpha_i$. But if no sequence has n terms, then eliminate every sequence whose initial member σ_{j+1} has a subscript $j+1$ which is the same as the subscript of some member of another sequence. There will remain exactly n of the σ 's,

$$\sigma_1^{(a_1)}, \sigma_2^{(a_2)}, \dots, \sigma_n^{(a_n)}$$

whose superscripts have the property

$$\begin{aligned} \alpha_{i+1} &= \alpha_i + 1 & \text{when } \sigma_i^{(a_i)} > 0, \\ \alpha_{i+1} &= 1 & \text{when } \sigma_i^{(a_i)} \leq 0. \end{aligned} \quad (10)$$

Then the only *AP* consistent with the given *SP* will be given by

$$y_i = \sigma_i^{(a_i)}. \quad (11)$$

Return now to the case when all fibers are excited, which occurs whenever a sequence (8) exists having no negative members. The determinant of equations (7) in the case when all α 's are non-null is equal to

$$\Delta = 1 - a_1 a_2 \cdots a_n, \quad (12)$$

as is easily verified, and the solutions in this case are

$$y_i = \sigma_i^{(n)} / \Delta. \quad (13)$$

But every $y_i > 0$ and at least $\sigma_{j+n}^{(n)} > 0$. Hence $\Delta > 0$, which means that the parameters a_i cannot be too large or the fibers too active. This apparent paradox simply means that if the activity parameters a_i are too large and the fibers too active, then if all fibers were set into activity at once the excitation would build up beyond the point at which the linear approximation can be retained. Hence

For a circuit of only excitatory fibers the linear approximation does not give a steady state for the case when all the fibers are active if the product of the activity parameters a_i exceeds unity.

A further lemma is almost immediate and will prove useful in later investigations.

If, for a given SP applied to the synapse of a simple circuit, there are two distinct AP's both consistent with this same SP, then every a_i which is zero in the one must of necessity be non-zero in the other. That is to say, if a given set of constant stimuli S_i applied to the synapses of the circuit is capable of leading to either of two distinct AP's according to the order or manner of application of the S_i , then every fiber which is inactive in the one case is necessarily active in the other.

This is vacuously true when the circuit contains no inhibitory fibers. But in any case if there is an inactive fiber in a given AP, then its removal from the circuit would have no effect upon the AP or the EP of the remaining system, which is now a simple chain. But for a chain the SP determines uniquely the AP and the EP, so that the statement of the lemma follows.

We conclude these preliminaries with a brief consideration of the circuit of two fibers. We have to consider the quantities

$$\sigma_1^{(1)} = \sigma_1, \quad \sigma_1^{(2)} = \sigma_1 + a_2 \sigma_2,$$

$$\sigma_2^{(1)} = \sigma_2, \quad \sigma_2^{(2)} = \sigma_2 + a_1 \sigma_1.$$

If σ_1 and σ_2 are both non-positive no activity is possible, but if at least one is positive then at least one fiber must be active. Hence on account of the lemma just proved, if for a given SP there are two distinct AP's both consistent with this SP, they can only be described by the values $(a_1, 0)$ and $(0, a_2)$ respectively of (α_1, α_2) , for it can be shown that the AP (a_1, a_2) is not consistent with either of these. The first AP is associated with the EP $y_1 = \sigma_1 > 0$, $y_2 = \sigma_2 + a_1 \sigma_1 \leq 0$; the second with $y_2 = \sigma_2 > 0$, $y_1 = \sigma_1 + a_2 \sigma_2 \leq 0$. We inquire, therefore, whether

for any choice of the S_i , or, what comes to the same thing, of the σ_i , the four inequalities

$$\sigma_1 > 0, \quad \sigma_1 + a_2 \sigma_2 \leq 0,$$

$$\sigma_2 > 0, \quad \sigma_2 + a_1 \sigma_1 \leq 0,$$

may hold simultaneously. If $a_1 < 0$, $a_2 < 0$, and $a_1 a_2 > 1$, then in the (σ_1, σ_2) - plane it is readily verified that the ray $\sigma_2 + a_1 \sigma_1 = 0$ in the first quadrant lies above the ray $\sigma_1 + a_2 \sigma_2 = 0$ in the same quadrant, and that any choice of the σ 's in the angular region between these rays will satisfy the above inequalities. For such a circuit so stimulated either of two different activity patterns $(a_1, 0)$ and $(0, a_2)$ may occur. But if either of the three inequalities on the a 's fails then the SP determines uniquely the AP and the EP .

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STUDIES IN THE MATHEMATICAL BIOPHYSICS OF DISCRIMINATION AND CONDITIONING II: SPECIAL CASE: ERRORS, TRIALS, AND NUMBER OF POSSIBLE RESPONSES

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A special case of a problem discussed in a previous paper is treated in greater detail. An equation in the three variables, errors, trials and number of possible choices, is developed and compared with the results of an experiment performed under conditions closely approximating those required for the development of the equation. The agreement is excellent.

The development of a mechanism for discrimination and conditioning has been given elsewhere, and relations have been derived for special cases (Landahl, 1941, hereafter referred to as A). Here, we wish to consider a special case, involving only the variables, trials, errors, and the number of possible choices, N . The variation with N was discussed very briefly in A. We continue to use the same notation.

Instead of a choice between two stimuli, let there be a choice from among N stimuli, $\dots S'_i \dots$. The stimuli are assumed to have the same initial stimulus values, so that experimentally all bias is averaged out. The general case can be treated but with considerably more difficulty. Let ε_0 represent the initial excitation factor value of any one of the stimuli acting on the mechanism. Let one of these stimuli S'_c be positively associated with a stimulus S_c , outside the primed group of stimuli, so that if c is the number of correct responses, then ε_c , the stimulus value for S'_c , is given by [A, equation (11)]

$$\varepsilon_c = \varepsilon_0 + bc, \quad (1)$$

where $b = B f(t)$ in equation (11) of A.

Let us next assume that the stimuli of the primed group, among which a choice is made, other than S'_c , are negatively conditioned to S_c . If β' is a positive constant analogous to b , and if w_i is the number of responses to some item S'_i produced by S_c , then the stimulus for S'_i is given by

$$\varepsilon_{w_i} = \varepsilon_0 - \beta' w_i. \quad (2)$$

We wish, however, to consider only the correct and wrong responses in general and not wrong responses to particular stimuli. Hence, we obtain the average of the stimulus value for the wrong stimuli, and designate this value by ε_w . Summing equation (2) over i for the $N-1$ stimuli, we have for the average value ε_w ,

$$\varepsilon_w = \frac{1}{N-1} \sum_i \varepsilon_{wi} = \varepsilon_0 - \frac{\beta'}{N-1} \sum_i w_i. \quad (3)$$

As, $\sum w_i = w$, the total number of wrong responses, equation (3) becomes

$$\varepsilon_w = \varepsilon_0 - \beta w, \quad (4)$$

where $\beta = \beta'/(N-1)$. Here β is not analogous to b of equation (1).

When we neglect failures to respond, we have

$$n = c + w, \quad (5)$$

where n is the number of trials.

If P_{c1} is the probability corrected for chance that the choice is correct, we have from previous development [Landahl, 1938, equations (10) and (15)]

$$\log(1 - P_{c1}) = -k(\varepsilon_c - \varepsilon_w) = -k(b c + \beta w). \quad (6)$$

The relation between P_{c1} and P_c , the probability for a correct response (not corrected for chance) is given by [Landahl, 1939, equation (29)]

$$P_{c1} = \frac{N}{N-1} (P_c - \frac{1}{N}). \quad (7)$$

But we also can write instead of P_c ,

$$P_c = \frac{dc}{dn}, \quad (8)$$

since we identify P_c with the instantaneous rate of making correct responses. Thus, introducing (8) into (7) and the result into (6) and using (5), we obtain

$$\frac{dw}{dn} = 1 - \frac{dc}{dn} = \frac{N-1}{N} e^{-k(\beta w - b c + \beta n)}. \quad (9)$$

Integrating equation (9) and setting the initial conditions as $c = w = n = 0$, and solving for w , we obtain

$$w = \frac{1}{k(b - \beta)} \log \frac{N b}{(N-1)(b - \beta) e^{-k \beta n} + (N-1)\beta + b}. \quad (10)$$

We shall consider two special cases of equation (10). First let us neglect the effect of the negative conditioning so that $\beta = \beta' = 0$. Then

$$w = \frac{1}{kb} \log \frac{N}{(N-1)e^{-kbn} + 1}, \beta = 0. \quad (11)$$

Under certain conditions one might plausibly expect that $\beta' = b$, that is, the positive and negative learning are equally effective. In this case $\beta' = b = (N-1)\beta$. Then

$$w = \frac{N-1}{N-2} \frac{1}{kb} \log \frac{N}{(N-2)e^{-kbn} + 2}, \beta = \frac{b}{N-1}. \quad (12)$$

The equations which have been used hold well enough for probabilities not much greater than chance. For large probabilities of a correct response, error is introduced by assuming that we may use $\varepsilon_c - \varepsilon_w$. This value is too large as only those values of ε_{w_i} near ε_c have much influence. Thus P_c is overestimated. On the other hand, for large P_c , the approximation of a Gaussian distribution by an absolute value exponential curve [Landahl, 1938, equations (6) and (7)] underestimates the value of P_c . As these two errors, which occur at large values of P_c , tend to cancel out, we may hope for a rather good fit.

We shall now discuss the relation of the above equations to experiment, but first mention reasons for using the particular procedure which is described below. One is that a solution was found for this case, and the experiment was thus adapted to fit as closely as possible the theoretical assumptions. But also, as the development in A is made with particular reference to comparative data, and as we are here treating a special case of the more general development we have recognition rather than recall learning. The procedure could perhaps have been adapted to obtain both results at once, as also the theory; but this was not done.

One hundred and twenty pairs of four letter words were prepared in groups of four, eight and twelve—eight groups of four, five groups of eight, and four groups of twelve. The words were paired with some care, and there were no duplicates in the two hundred and forty words. Of each pair of words, we may refer to one as the stimulus word (S) and the other as the response word (S'). For each of the groups of four, eight and twelve response words two cards were prepared, each containing the same (four, eight or twelve) words, arranged in a different order. Alternate cards were used so that the effect of position on the response card would be largely eliminated

and also to prevent the subject from using some system in learning based on position. The stimulus words in each group were written on individual cards.

One subject was given six sittings at each of which twenty pairs of stimuli were presented sixteen times. Only one sitting was given in one day. Since the rate of presentation of items was approximately constant, the average time between an item and its repetition was the same for each of the groups (four, eight and twelve), and the same in each of the sixteen trials (about seven minutes).

For a particular sitting the subject was given a group of eight and a group of twelve pairs of words. For any trial the eight or twelve group was chosen at random to be first. If the eight group was chosen first for a particular trial, one of the two response cards (identical except for arrangement) was presented to the subject. A card containing a stimulus word from the corresponding group was chosen at random from among the eight stimulus words and presented. The subject had been told that for each stimulus word there was one word on the response card which was to be associated with it, and that he was to determine the correct response word in each case by trial and error. He was given but one chance to respond to a stimulus word in a particular trial, each of which consisted of twenty responses. He was to remember to give correct responses and to avoid wrong responses on successive trials. The response was verbal. The experimenter said "right" if the response word was paired with the stimulus word on the answer sheet for that group, if not, he said "wrong". After about ten seconds the next stimulus was presented. Immediately after the eighth item had been presented, the twelve group was similarly presented. One trial was thus completed in about five minutes. As the time the subject took to respond varied considerably with trials, the period between trials was varied, largely compensating for the former. This period was about two minutes, and was spent in reading or other activity of interest to the subject. The procedure was carried out to sixteen sets of trials of which the last three trials were errorless trials, except in two cases. The two exceptions were given extra trials.

The constants b and β' are functions of the time between repetitions as well as the average number of intervening presentations (in this case twenty). But this was constant throughout the three groups. However, these constants may also depend on the number in the group—four, eight or twelve. This would be possible, if within each group there was some sort of mutual inhibitory effect. The effect might also be present as an influence of one group upon another in the same sitting but the latter would be averaged out due to the vari-

ous combinations of three groups and to the random order of presentation. But the effect of stimuli within the group upon one another can show up if present. Hence $b = b(N - 1)$ in general. Now, if we assume some mutual inhibitory effect (cf. Rashevsky, 1938, Figure 54), b will decrease with N . But b must be positive or zero. Let us therefore somewhat arbitrarily assume the relation

$$b = \frac{\eta}{k} e^{-\zeta N}. \quad (13)$$

It must be kept in mind that the particular form of equation (13) is not as yet derived from the mechanism, but its general shape can be deduced. We shall find that we could almost as well use an equation of the form $b = \eta'(1 + \zeta'N)^2$ or $b = \eta'' - \zeta''N$. Equation (13) is somewhat more convenient and fits the data slightly better. However, the accuracy of the latter, and the presence of only three values of N do not warrant any choice as to the form of the $b(N)$ relation as long as it is a decreasing function. With more accurate data containing more values of N , this relation could be more accurately obtained.

As the subject was given an equal amount of time to remember a correct or wrong response, one might expect that $b = \beta'$, so that equation (12) should fit the data. However, the subject's report that he did not attribute much value to remembering the wrong responses, although instructed to do so, would justify the use of equation (11). It was found that equation (12) did not fit any one of the curves very well, so that equation (11) was used. In order to fit the three curves simultaneously, we must also use equation (13). Introducing this equation into equation (11), we have a two parametric surface in the variables w , n , and N :

$$w = \frac{e^{\zeta N}}{\eta} \log \frac{N}{(N - 1)e^{-\eta n e^{-\zeta N}} + 1}, \quad (14)$$

the parameters being η and ζ .

In Figure 1 are graphed the curves $w(n)$ as given by equation (14) for $N = 4$, $N = 8$, and $N = 12$, using the values $\eta = 1.15$ and $\zeta = 0.098$. The crosses, open circles and solid circles are the data for the respective groups, four, eight, and twelve. Each cross is a value based on thirty-two responses; each open circle is based on forty responses; and each solid circle is based on forty-eight responses. The ordinate represents the cumulative wrong responses for one stimulus; the abscissa represents the number of the trial; and N is the number of possible responses in the group. The agreement is better than would be expected. Even much poorer agreement would be meaning-

ful, since, we are treating a special case of a more general situation. A test, using different material, under different conditions, especially comparative data, would be desirable. Only then, if sufficiently close agreement is found, could the development be considered as satisfactory.

By taking a fixed value of N , we may find the relation between bk and such variables as time between presentations and effect of reward; and by using the more general equation (10) the ratio of b to β' can be obtained for varying degrees of reward and punishment.

It may be noted that it is the value bk which enters as a parameter—the product of b , the coefficient of conditioning, and k , the parameter of the distribution curve, k being approximately the reciprocal of the standard deviation. Thus, although b is independent of discrimination and k is independent of conditioning, we find that the final rate of learning is determined by the product of these two parameters, and b itself is a product of two parameters. Such a situation occurs frequently as in the various cases discussed in A.

If such data are available from a number of experimental situa-

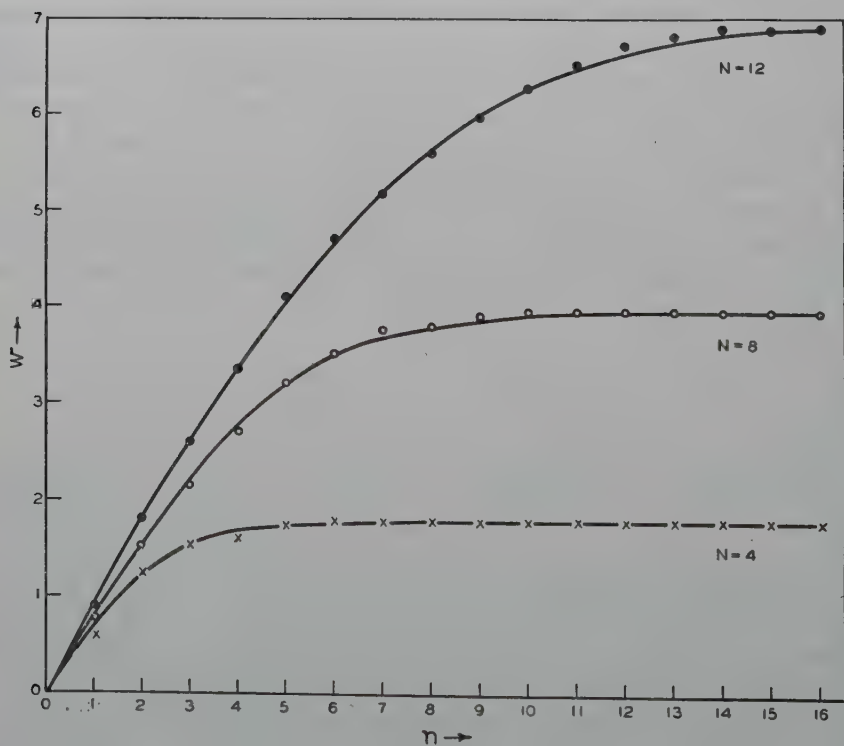


FIGURE 1

tions, it would be necessary to analyze the values involving products to obtain the separate parameters. If the data are available for a group of subjects, one can express the separate parameters as well as the products as deviates from the means. Expanding the result and retaining only the terms of first degree in the deviates, the expression for an experimental value is given as the sum of terms each of which is a coefficient times the deviate value of a basic parameter. This may be summed over all the parameters as the deviates are zero for those which are absent. Generally one would expect a particular experimentally derived value to involve only a limited number of the basic parameters, as is the case above. Thus we have the basic equation of factor analysis as well as a requirement of simple structure (Thurstone, 1935). The factor method might well be useful if such a stage is reached and if a simpler method is not possible.

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